water is never dominant in shock models; $H_2$ and CO always appear to be more important cooling species. This discrepancy must be resolved by further refining the current models if we want to understand the energy balance of the protostellar system.

As protostellar evolution proceeds, the circumstellar matter is gradually dispersed and the power of the outflow declines, but some of the original cloud material remains present in the form of a circumstellar disk. Gas excitation by the star's radiation field increasingly leads to the dissociation of water into OH and atomic oxygen, following the reverse reactions of Eqs. 1 and 2, over large regions (*9*). In dense circumstellar disks, however, part of the water produced during star formation can be deposited on dust grains, resulting in an enrichment of the disk material with water ice. In this form, water can remain unaltered until the disk evolves into a protoplanetary system, which may eventually form solid planetary bodies. ISO and SWAS could not measure the water content of protoplanetary systems because of insufficient spatial resolution; they were restricted to investigating regions no smaller than a few thousand astronomical units (AU) (1 AU is the distance between the sun and Earth) from the central star.

The ISO and SWAS observations of water in different environments during star formation have allowed chemical models of star formation to be tested for the first time. Instruments with higher spectral and spatial resolution will become available with space missions planned over the next decade, such as the Far Infrared and Submillimetre Telescope (FIRST) and the Next Generation Space Telescope (NGST). These missions may lift some of the remaining mysteries, particularly regarding the later stages of stellar formation, and may even provide insights into the likelihood of the development of life, which is crucially dependent on the availability of water.

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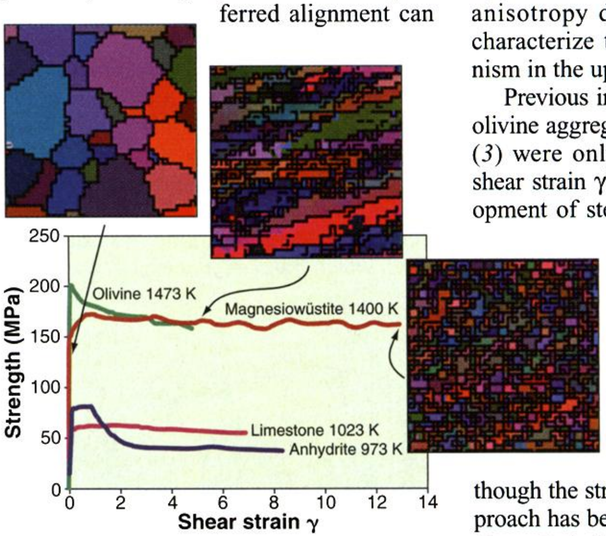
PERSPECTIVES: GEOPHYSICS

# Earth Under Strain

**Stephen Mackwell and David Rubie**

Heat is constantly transferred from Earth's hot interior to the surface through convection of the mantle. At Earth's surface, mantle convection drives plate tectonics, as manifested by earthquakes, volcanoes, and mountain building. When the slowly convecting mantle encounters regions that are less mobile, for example, at the bottom of the rigid plates, substantial amounts of shear strain may accumulate. On page 1564 of this issue, Bystricky *et al.* (*1*) illustrate how rock textures and mechanical behavior evolve during this type of deformation. The results can be correlated with measurements of seismic wave propagation through the mantle, providing fundamental insights into processes occurring in Earth's upper mantle.

Seismic waves travel through Earth's interior as compressional waves, where the particle motion is parallel to the propagation direction of the wave, or shear waves, where the particle motion is perpendicular to this direction. When shear waves are detected at the surface, they can be resolved into two components at right angles to each other. Numerous seismological studies have demonstrated that in the shallow mantle below the oceans, the component of shear waves parallel to the direction of plate motion is often faster than that perpendicular to that direction (*2*). The difference in velocity leads to shear-wave splitting, such that one component arrives at the seismic station in advance of the other. This different behavior for parallel and perpendicular waves is due to the preferred crystallographic alignment of minerals that have anisotropic (direction-dependent) elastic properties. Such a preferred alignment can be induced during plastic deformation by dislocation creep, where motion of crystal dislocations along planes in the mineral grains results in straining of the rock (*2*).



**Unexpected behavior.** Rocks composed of different minerals show substantial variation in mechanical behavior and textural evolution when deformed to high strains in simple shear. The plot shows evolution in strength of the various rock types with increasing shear strain. Data from (*1*, *6-8*). The digital scanning electron microscopy images of the grain texture of magnesiowüstite samples show evolution of microstructure with increasing strain. The images are 250 μm wide.

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As Bystricky *et al.* (*1*) show, shear deformation of a rock composed predominantly of olivine, the major upper mantle mineral, results in a preferred orientation of one particular crystallographic axis parallel to the shear direction. This observation is consistent with seismic observations of shear-wave splitting in the oceanic upper mantle. The new results (*1*), however, also demonstrate that use of the seismic anisotropy data alone cannot uniquely characterize the dislocation creep mechanism in the uppermost mantle.

Previous investigations of the textures in olivine aggregates during shear deformation (*3*) were only performed to a maximum shear strain γ of 1.5, too low for the development of steady-state textures and deformation behavior. The powerful experimental technique applied by Bystricky *et al.* (*1*) applies a torsional stress to the sample, allowing shear deformation to large strains (*4*) that appear to reproduce mantle temperatures and strains reasonably well (although the strain rates are too fast). This approach has been used to investigate the high shear strain behavior of rocks composed of olivine (*1*), marble (*5*), limestone (*6*), anhydrite ($CaSO_4$) (*7*), and magnesiowüstite [(Mg,Fe)O] (*8*). The textural and mechanical evolution of rocks made of these minerals with increasing shear strain is quite varied (see the figure). Limestone (*6*) shows little change in strength or texture and continues to deform even at high strains by diffusional creep, where diffusion of atoms along

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grain boundaries results in straining of the rock. In contrast, anhydrite aggregates (*7*) decrease substantially in strength at a shear strain of about $\gamma = 1$. This drop in strength results from a change in deformation mechanism from dislocation creep to diffusional creep as the grain size of the rock is reduced by dynamic recrystallization. Marble and magnesiowüstite aggregates (*5*, *8*) show no change in deformation mechanism and little change in strength with increasing strain, despite recrystallization to a substantially finer grain size. After reaching a peak at modest strains, the strength of olivine aggregates (*1*) decreases as the grains recrystallize to a finer grain size. No change in deformation mechanism is observed.

All these rocks thus show substantial changes in microstructure and texture during deformation, with large reductions in grain size, but the deformation mechanism changes in only one of the materials (anhydrite). It should therefore not be assumed that recrystallization and associated grain-size reduction during high-strain deformation in Earth's interior will necessarily result in changes in deformation mechanism (*9–11*).

Many modeling studies of the deformation of Earth's upper mantle use the rheological data of Karato *et al.* (*10*), which were collected during low-strain deformation experiments of olivine aggregates in both dislocation and diffusional creep fields. No changes in deformation mechanism due to dynamic recrystallization were observed experimentally, but these results have nevertheless been used to predict mechanism changes due to recrystallization as a function of depth in the upper mantle (*11*).

The new results (*1*), albeit collected over a limited range of experimental conditions, show no such changes in deformation mechanism for olivine-dominated rocks despite substantial grain-size reduction. Ultimate resolution of the question as to whether grain-size reduction by dynamic recrystallization changes the deformation mechanism in the upper mantle must await further experimental data covering a broader range of conditions. Until then, we should be careful not to invoke deformation mechanisms for which there is no definitive evidence.

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**PERSPECTIVES:** SIGNAL TRANSDUCTION

# An Arresting Start for MAPK

**Jacques Pouysségur**

Protein kinases are ubiquitous enzymes that are able to modulate the activities of other proteins by adding phosphate groups to their tyrosine, serine, or threonine amino acids (phosphorylation). Mitogen-activated protein kinases (MAPKs), which are activated by many different signals, belong to a large family of serine/threonine protein kinases that are conserved in organisms as diverse as yeast and humans. MAPKs deliver extracellular signals from activated receptors to various cellular compartments, notably the nucleus, where they direct the execution of appropriate genetic programs. A unique feature of MAPKs is that they themselves can be activated by addition of phosphate groups to both their tyrosine and threonine amino acids (dual phosphorylation) after stimulation of a receptor by growth factors, mitogens, hormones, cytokines, or environmental stresses. MAPKs operate in modules composed of three protein kinases that phosphorylate and activate each other sequentially: MAP kinase kinase kinase (MKKK) activates MAP kinase kinase (MKK), which then activates MAP kinase. These kinase modules have been duplicated with slight variations, allowing cells to instigate multiple biological responses through a set of MAP kinase–wiring networks.

The coexistence of conserved protein kinase modules within the same cellular compartment, however, poses an enormous challenge for the cell because protein kinases are rather promiscuous enzymes. How does the cell solve the crucial problems of substrate specificity and the prevention of inappropriate cross talk between signaling pathways? How are these highly conserved signaling circuits "insulated" from nonspecific interactions with other molecules? Cells seem to have adopted two solutions. The specificity and fidelity of kinases is ensured by the existence of specific docking sites on kinases and their protein substrates (*1*, *2*). Insulation and signal efficiency are provided by scaffold proteins that assemble the components of a given MAPK module into a single signaling complex (*3*). Attempts to identify scaffold proteins have been frustrated by the fact that they are not enzymes and seem to have emerged as nonconserved evolutionary "bricolage." The first MAPK scaffold protein identified was Ste5 in budding yeast. An astonishing and intriguing new example of a mammalian scaffold protein is presented by McDonald *et al.* (*4*) on page 1574 of this issue. The investigators provide evidence that this new scaffold protein, β-arrestin 2, brings together components of the MAPK module, resulting in activation of c-Jun amino-terminal kinase–3 (JNK3) in response to activation of G protein–coupled receptors (GPCRs).

The β-arrestin 2 scaffold protein is not homologous to c-Jun amino-terminal kinase interacting protein (JIP), a member of the mammalian JNK scaffold protein family (*3*). This discovery is intriguing because for years it has been known that arrestins stop signals from growth factors, hormones, or environmental stressors by uncoupling the activated GPCR from its G protein signaling molecule (*5*, *6*). But how can arrestins be both "Stop" molecules and signal activators? What is the evidence that arrestins are scaffold proteins for the MAPK module that activates JNK3 through the activation of ASK1 and MKK4?

With a yeast two-hybrid screening assay, McDonald *et al.* identified a direct interaction between β-arrestin 2 and the carboxyl-terminal portion of JNK MAPK family members, in particular with the p54 splice variants of JNK. Immunoprecipitation of β-arrestin 1 and 2 from extracts of cultured cells expressing epitope-tagged JNK1, JNK2, and JNK3 isoforms established that only β-arrestin 2 coimmunoprecipitated with the JNK3 isoform. The authors then explored the functional consequence of this interaction on JNK3 activation by measuring phosphorylation of c-Jun, a typical transcription factor targeted by the JNK signaling pathway. JNK3 phosphorylated c-Jun only when it was coexpressed in cultured cells with both β-arrestin 2 and ASK1 (an upstream MKKK activator of the pathway). Because ASK1 cannot directly activate JNK3, this result suggested that MKK4 or MKK7 is present in the complex and that β-arrestin 2 may serve as a scaffold pro-

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